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Impact of a Castrating Trematode, *Neophasis* sp., on the Common Whelk, *Buccinum undatum*, in the Northern Gulf of St. Lawrence

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Abstract. We observed heavy trematode infections of whelks, *Buccinum undatum*, from the Mingan Islands, eastern Canada, by larval stages of a species of *Neophasis*. Only sexually mature whelks were infected, 23% of mature females and 15% of mature males, and prevalence increased rapidly with whelk size. In most cases the parasite completely occupied the gonad, causing castration. The digestive gland was also infected, although to a lesser degree (0% to 50% occupation), and a marked reduction in the mass of the penis was associated with the infection. A decrease in the proportion of whelks with a highly infected digestive gland between May and August 1994 suggested mortality of infected individuals. Whelks held for 12 to 15 months in the laboratory retained the infection but did not show significant mortalities (possibly because food was abundant and predators absent). The larval stage of *Neophasis* sp. found in whelks was a cercaria; however, the tail easily detached. The putative infective stage (metacercaria) was not observed but may be present in whelks in late winter and early spring. Other trematode parasites observed were adult *Steringophorus furciger* in the stomach and larval *Renicola* sp. in the digestive gland.

Introduction

Parasitic castration is the partial or total inhibition of gametogenesis of a host species due to the activity or physical presence of a parasite (Cheng, 1983). Many larval trematodes castrate their gastropod hosts (Cheng, 1964; Lauckner, 1986), and gigantism and modifications of secondary sexual characteristics may also occur (Rothschild, 1936, 1941; McClelland and Bourns, 1969; Mouritsen and Jensen, 1994; Gorbushin, 1997). Because castrating parasites may decrease the number of breeding individuals within gastropod populations (Kuris, 1973, 1974; Lauckner, 1986), infected populations may show declines or strong fluctuations in abundance (Lie, 1973; Combes, 1982; Lauckner, 1986; Huxham *et al.*, 1993; Lafferty, 1993).

Køie (1969) identified four castrating larval trematodes in a Danish population of the common whelk, *Buccinum undatum* L. 1758: (1) *Zoogonoides viviparus* (Olsson, 1868) Odhner, 1902; (2) *Neophasis anarrhichae* (= *N. lageniformis*) (Nicoll, 1909) Bray, 1987; (3) *Cercaria buccini* (Lebour, 1911); and (4) an unidentified species of *Renicola*, Cohn, 1904. The first three are found in both the gonad and digestive gland and the fourth only in the digestive gland. Infections by *Z. viviparus* and *N. anarrhichae* result in a light grey appearance of the infected organs, whereas *C. buccini* does not affect the color of the infected organs (Lebour, 1911), and *Renicola* sp. forms light yellow bodies in the digestive gland. Other parasites of *B. undatum* identified by Køie (1969) are the turbellarian commensal *Graffilla buccinicola* (Jameson, 1897), found in the digestive gland and stomach, and the trematode *Steringophorus furciger* (Olsson, 1867) Odhner, 1902, present only in the stomach. Hamel (1989) observed larval trematode parasites in the gonad and digestive gland of 15% of adult *B. undatum* in the Mingan Islands, Gulf of St. Lawrence, eastern Canada, and indicated that the characteristics of the infection were similar to those described by Køie (1969) for *Z. viviparus* and *N. anarrhichae*.

In our study we identified one trematode in *B. undatum* as

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belonging to the genus *Neophasis*, which has life cycles involving one or two intermediate hosts (gastropod, fish) and a teleost final host (Bray and Gibson, 1991). Caudate cercaria develop in the gastropod, become free-living, and encyst as metacercaria in bivalve molluscs and fish that are later preyed upon by the final fish host. In *Neophasis anarrhichae*, *B. undatum* apparently serves as the only obligate intermediate host. Caudate cercariae develop within rediae in the whelks. The cercarial tail is shed within the redia, and the noncaudate cercaria is considered a metacercaria that does not encyst (Koie, 1973). Final hosts are carnivorous teleosts belonging to the genus *Anarhichas*, which acquire the parasite by preying on infected whelks. Encysted metacercariae of an unidentified *Neophasis* have been reported on the mesentery of American plaice, *Hippoglossoides platessoides*, and in the gut of Atlantic cod, *Gadus morhua*, from Canadian waters (Appy and Burt, 1982). Bray and Gibson (1991) indicated that this immature trematode may be *Neophasis burti* Bray and Gibson, 1991.

Buccinum undatum is the most abundant carnivore in the benthic community in the Mingan Islands in the northern Gulf of St. Lawrence (Jalbert *et al.*, 1989; Himmelman, 1991). It is also of commercial importance in the Gulf of St. Lawrence and St. Lawrence Estuary. From 1991 to 1993, 700 metric tons of whelks were harvested annually in Quebec and 30% of this harvest came from the Mingan Islands (Savard, 1994).

Several characteristics of the biology of the common whelk make it especially vulnerable to fishery over-exploitation. First, recolonization of over-exploited sites is likely to be slow because the whelk lacks a pelagic larval stage and adults move only by crawling. Further, stocks are limited by a slow growth rate. In the Mingan Islands, whelks attain a shell length of 75 to 80 mm, the size at sexual maturity, in 6 to 8 y (Martel *et al.*, 1986; Savard, 1994). At present the fishery is not limited by a minimal capture size. In 1993, 25% of whelks collected measured <75 mm (Savard, 1994) and thus had not reproduced. A decrease in the average size of harvested whelks has been recorded in several fishery zones and may indicate over-exploitation. Although such a decrease has not yet been observed in the Mingan Islands, it is likely to happen given the intensity of the fishery.

The objective of our study was to identify parasites of the common whelk, *Buccinum undatum*, in the northern Gulf of St. Lawrence and to evaluate their impact on the whelk. We sampled a large number of whelks during two periods in summer 1994 to determine the prevalence of parasites (proportion of whelks infected) and to quantify their effects on different body organs. In addition, we studied morphological changes in parasites over time in the laboratory. Finally, we exposed American plaice to larval *Neophasis* sp. from *B. undatum* to determine whether larval *Neophasis* would develop and mature to the adult stage and thus permit identification to species.

Materials and Methods

We sampled whelks from the Mingan Islands (50° 35′ N, 63° 35′ W), in the northern Gulf of St. Lawrence (Fig. 1). Using scuba, we collected all whelks (buried and unburied) that measured 10 to 110 mm in shell length and were found within 1 m of either side of two 160-m long transects parallel to the shoreline at Cap du Corbeau on Île du Havre, one at 6 m and the other at 15 m in depth. Whelks were abundant on the sediment bottom in this area. We collected 327 whelks in May 1994 and 313 in August 1994.

All whelks were frozen, and later dissected to identify and determine the prevalence of parasites. After measuring the shell length of each animal, we fragmented the shell with a hammer to remove the soft tissues intact. Then, the gonad, penis, remaining reproductive organs, digestive gland, and other body components were separated and weighed (after draining on paper toweling for 10 min). A dissecting microscope was used to examine each organ for parasites. In examining the gonad and digestive gland, we pressed the tissues between two 7.5 × 7.5 cm glass plates to facilitate the search for parasites, and visually estimated the proportion of the organs occupied by parasites (the larvae were too abundant to be counted). Samples of larvae found in each infected whelk were isolated and preserved in AFA

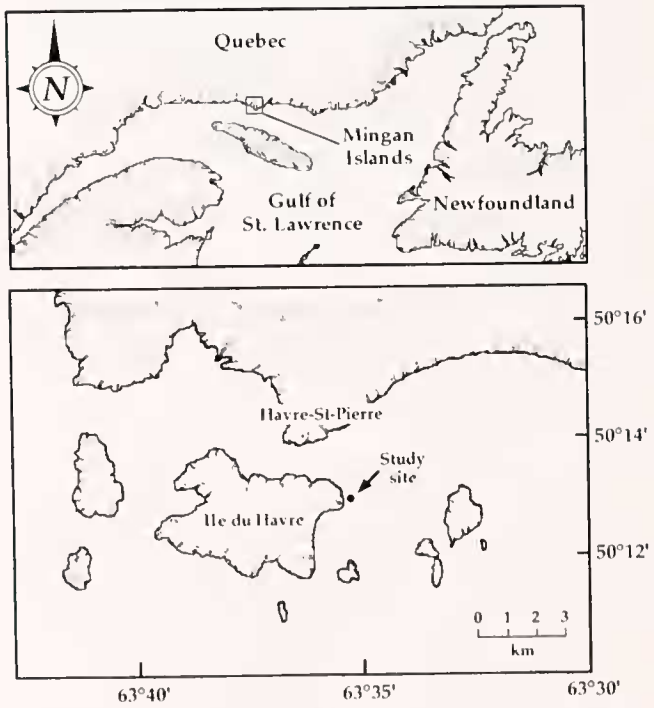

Figure 1. Location of the study site, Cap du Corbeau, in the Mingan Islands in the northern Gulf of St. Lawrence, Canada.

(a solution of alcohol, formalin, and acetic acid; Pritchard and Kruse, 1982) for later identification.

We identified parasites to genus based on the morphology of different stages. Preserved parasites were examined with a microscope, first without staining and then using Scheider's acetocarmine stain (Pritchard and Kruse, 1982). Further, to obtain the adult stages required for species identification of larval parasites from the gonad and digestive gland, we attempted to infect American plaice, *Hippoglossoides platessoides*, which is a host for several trematodes (Bray and Gibson, 1991). Plaice, measuring 15 to 20 cm in total length, were collected in June 1994 by trawling at a depth of 53 m near Matane (48° 53′ N, 67° 19′ W) in the St. Lawrence Estuary. In November 1994, using forceps, we placed pieces of infected gonad, from freshly killed whelks (collected in the Mingan Islands in October 1994), into the stomachs of six plaice. The plaice were first anesthetized by placing them for 1–3.5 min in 2 l of seawater containing 0.3 g of tricaine methanesulfonate (MS-222). Following treatment, the plaice were kept in well-oxygenated water for 24 h to recuperate. The six exposed plaice were maintained at 25‰ to 28‰ salinity and 4.4° to 10.4°C for 10 to 20 d in a 130-l tank at the Maurice-Lamontagne Institute. Four other nonexposed plaice, which served as controls, were maintained under the same conditions in another 130-l tank. After 10 to 20 d, the plaice were killed by cervical dislocation, dissected, and examined for intestinal trematodes.

We also examined changes in parasitic infections over time in 80 whelks measuring 80–110 mm in shell length. These specimens were collected in October 1994 from along the same two transects at Cap du Corbeau, and using the same methods, as in May and August. These whelks were maintained at 25‰ to 28‰ salinity and 4.4° to 10.4°C in two 130-l tanks until January 1996. Using the technique described above, we examined a first sample of 30 whelks in November 1995 and a second sample of 45 whelks in January 1996. Five whelks died during this laboratory study and were frozen for later examination. We recorded the size of cercariae and rediae in whelks collected from the field in May and August 1994, and from the laboratory sampling in November 1995 and January 1996, from images projected through a drawing tube attached to a Leitz diaplan (×40) microscope using a digitizer and computer (using Sigmascan image analysis software, version 3.90; SPSS Inc., Chicago, IL).

To evaluate the influence of sex and sampling period (May and August) on the prevalence of parasites in gonadal and digestive gland tissues, and on the proportion of these organs infected, we applied log-linear models adjusted to three-dimensional contingency tables (Legendre and Legendre, 1984). Only significant models were retained, and the best model describing the data was determined using the partitioning method. For the analysis of prevalence, only sexually mature whelks (>75 mm in shell length; Martel *et al.*, 1986) were used since parasites were absent in immature whelks. Because the proportion of the gonad and digestive gland occupied by parasites varied markedly, different categories were used for the two organs: 0%–90% and 90%–100% classes for the gonad and four 25% classes for the digestive gland. All statistical analyses were performed using the BMDP4F statistical program (Dixon, 1985).

We compared the somatic mass and shell length of the parasitized and nonparasitized whelks with a Mann-Whitney U test. To eliminate the confounding effect of parasitism on reproductive organs and the digestive gland, we used eviscerated mass, defined as the total mass minus the mass of the digestive gland, gonad, penis, and remaining reproductive organs. Given the slow growth of whelks, we assumed that there was no impact of sampling period on eviscerated mass and shell length and therefore pooled the May and August samples for the analyses.

Because the number of opercular striae can be used as an estimate of age of *B. undatum* (Santarelli and Gros, 1985), we used these striae to evaluate whether the age of infected and noninfected whelks was different. We compared the number of operculum striae of infected and noninfected whelks using Mann-Whitney U tests.

To evaluate the effect of parasites on the penis, we compared penis mass of infected and noninfected whelks, in May and again in August, using Mann-Whitney U tests. To determine the effect of the parasite on penis mass, we first determined the regression of penis mass to shell length for noninfected whelks and then calculated the deviation in penis mass of infected whelks compared to this relationship. As the distribution of residuals was normal, a Student's t test was used to test the hypothesis that the mean of the residuals was equal to 0 (Zar, 1984); a value different than 0 ($P < 0.05$) would indicate that the parasite affected penis mass.

Results

Identification of parasites in the gonad and digestive gland

Our examination of whelks collected in May and August 1994 in the Mingan Islands revealed that cercariae and rediae of one species of trematode infected both the gonad and the digestive gland. The cercariae possessed an oral sucker at the anterior portion of the body and a ventral sucker in the middle of the body (Fig. 2A). They also possessed a straight, nonfurcate tail and eyespots located anterolateral to the oral sucker. Rediae had only an oral sucker and a small pharynx in the anterior portion of the body (Fig. 2B). The shape of the cercariae varied in different seasons. Cercariae were most elongated in August 1994 (mean length = 395 μm; mean width = 70 μm) and least in January 1996 (mean length = 199 μm; mean width = 98 μm). The tail was easily detached in May but not on the other dates. Rediae were cylindrical and less variable in

Figure 2. Stages of the trematode *Neophasis* sp. from live tissues of the whelk *Buccinum undatum*. (Top) A cercaria with eyes and a straight, nonfurcate tail. (Bottom) A redia containing several cercariae.

shape over time than cercariae. They were longest in August 1994 (mean length = 2190 μm) and shortest in November 1995 (1325 μm). In May and August 1994 some rediae did not contain cercariae, whereas in November 1995 and January 1996 all contained cercariae.

The presence in the cercarial stage of eyes at the anterior portion of the body and a straight, nonfurcate tail placed this parasite in the genus *Neophasis* (Stafford, 1904). Our identification to genus was confirmed by Dr. R. A. Bray at the British Museum of Natural History London (pers. comm.). We found no adult *Neophasis* in the digestive systems of the American plaice (*Hippoglossoides platessoides*) that we had attempted to infect, and thus we could not identify the species of *Neophasis*.

In noninfected whelks, the gonads were yellow to orange in color, and the digestive gland was brown (Fig. 3A, B). In contrast, the gonad and digestive gland of whelks infected with larval *Neophasis* sp. were light grey (Fig. 3C, D), owing to the color of the cercariae and rediae that replaced the tissues. Larvae of *Neophasis* sp. were also found in other reproductive organs—the albumin gland of females and the seminal vesicle of males.

Prevalence of Neophasis *sp. in whelks in the field*

Larvae of *Neophasis* sp. were present only in sexually mature whelks (Fig. 4). Three of the log linear models (Table 1) testing the effect of sex (S) and sampling date (M) on prevalence (P) were significant ($\alpha = 0.05$); of these, Model B, lnE = P + S + M + SM + PS, best described the data (Table 1). This model indicated that only sex influenced prevalence. Female whelks were more infected ($P = 0.05$) by larval *Neophasis* sp. than were males (22.9% *vs.* 15.4%). In both sexes, prevalence markedly increased with increasing whelk size and exceeded 90% for whelks measuring more than 90 mm in shell length.

The infected whelks were the largest (Figs. 4, 5) and also seemed to be oldest (Fig. 5). Shell length was greater for infected than noninfected whelks (Fig. 5; females: $U = 14.02$, $n = 218$, $P < 0.001$; males: $U = 12.40$, $n = 246$, $P < 0.001$), and the same trend was indicated for eviscerated mass, although it was significant only in males (Fig. 5; females: $U = 1.3$, $n = 218$, $P = 0.25$; males: $U = 6.96$, $n = 246$, $P = 0.01$). Finally, the number of operculum striae tended to be greater for infected than noninfected whelks (Fig. 5; females: $U = 4.98$, $n = 77$, $P = 0.026$; males: $U = 3.69$, $n = 73$, $P = 0.055$).

Effects of Neophasis *sp. on the whelk*

In all cases, the gonad was the organ most infected by larval *Neophasis* sp. (Fig. 6). None of the models testing the influence of sex and sampling date on the proportion of the gonad occupied by parasites were significant. Thus, no differences between females and males or between the two sampling periods were indicated. In 97% of infected whelks, cercariae and rediae occupied more than 90% of the gonad. The one individual with a lower portion of the gonad infected by larval *Neophasis* sp. (20%) was a male collected in August 1994 (Fig. 6).

The proportion of the digestive gland infected with cercariae and rediae was much lower than for the gonad and exceeded 50% in only a few whelks (Fig. 6). Two log linear models (Table 1) testing the effect of sex and sampling date on the proportion of the digestive gland occupied by the parasite were significant ($\alpha = 0.05$), and the partitioning method indicated that Model B, lnE = O + S + M + OM + SM, best described the data (Table 1). This model indicated that only sampling period influenced the proportion of digestive gland occupied by the parasite. The proportion of the digestive gland occupied by larval *Neophasis* sp. in infected whelks dropped between May and August (Fig. 6). For example, 45% of the infected whelks had more than 25% of the digestive gland infected in May compared to 8% in August.

In both May and August, the regression of penis mass to shell length was positive for noninfected males (Fig. 7; May: $n = 122$, $r^2 = 0.26$, $P < 0.001$; August: $n = 93$, $r^2 = 0.29$, $P < 0.001$), but the mean residual penis mass of infected whelks compared to the regressions for noninfected whelks differed from 0 (May: $n = 21$, $t = 18.514$, $P <$

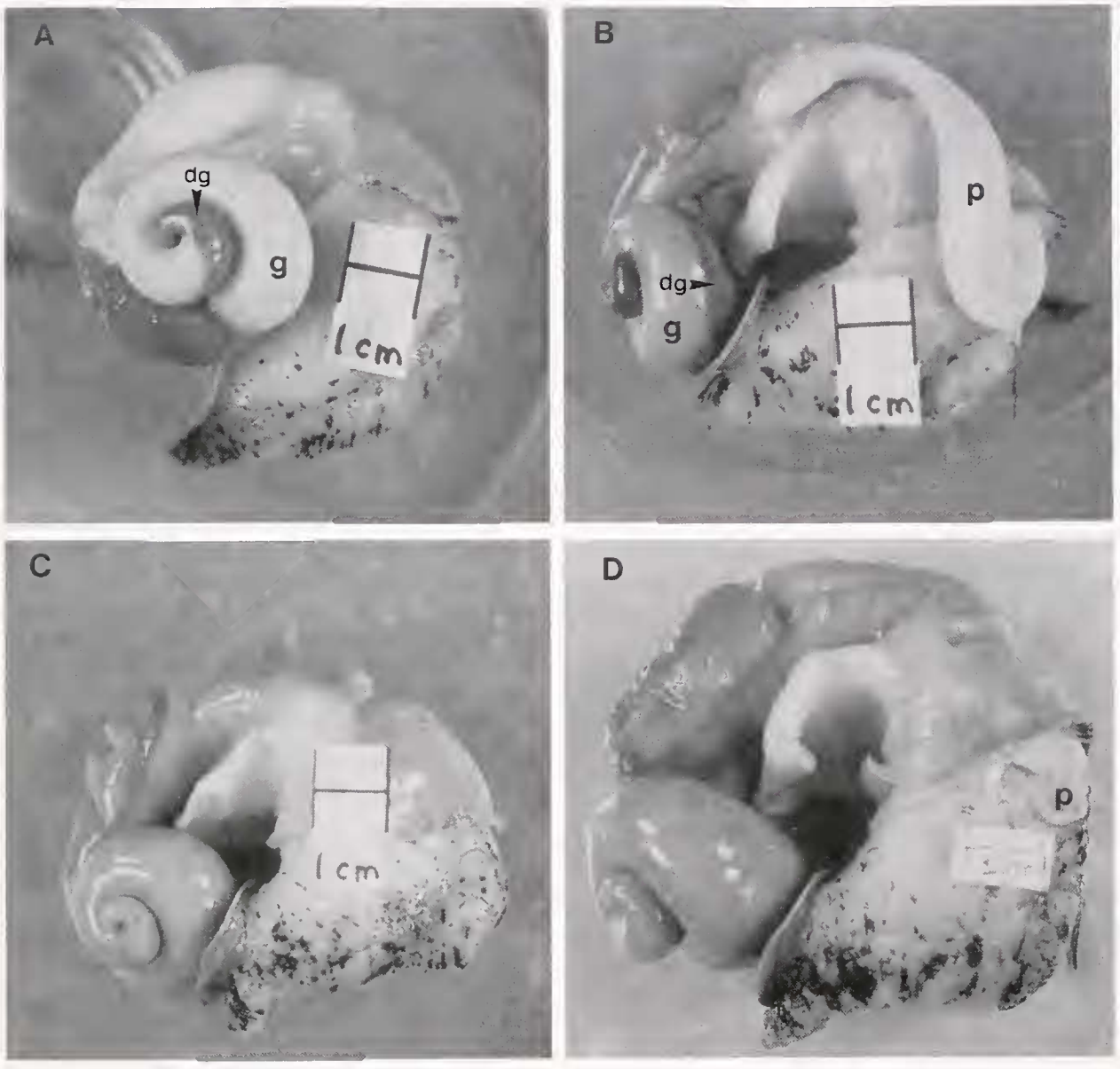

Figure 3. Whelks, *Buccinum undatum*, with the shell removed. The gonad (g) is clearly distinct from the digestive gland (dg) in the uninfected female (A) and male (B) because of different coloration, whereas these organs are less easily distinguished in the infected female (C) and male (D) because of similar coloration (light grey). Note the strong atrophy of the penis (p) of the infected male (D).

0.001; August: $n = 18$, $t = -6.427$, $P < 0.001$). Penis mass was markedly smaller for infected males (Fig. 7).

Neophasis *sp. infections in whelks in the laboratory*

Whelks sampled from the laboratory in November 1995, after 12 months in captivity, had larval *Neophasis* sp. in 20.0% of females (3/15) and 0% of males (0/15). In one of the three infected females, larval *Neophasis* sp. had invaded the gills and mucus gland tissues, a condition never observed in the whelks collected in May and August 1994 from the field. In January 1996, after 15 months in the laboratory, 17.4% of females (4/23) and 4.5% of males (1/22) were infected. The prevalence of *Neophasis* sp. in the laboratory whelks (dissected in November 1995 and January 1996) tended to be greater for females than males, but not significantly so (Fisher exact probability test, $P = 0.056$). For females, the prevalence in the laboratory was similar to that in the field sampling ($G = 0.39$, $n = 261$, $P = 0.53$), but was lower for males (Fisher exact probability test, $P = 0.039$). Five whelks died during captivity, and three of

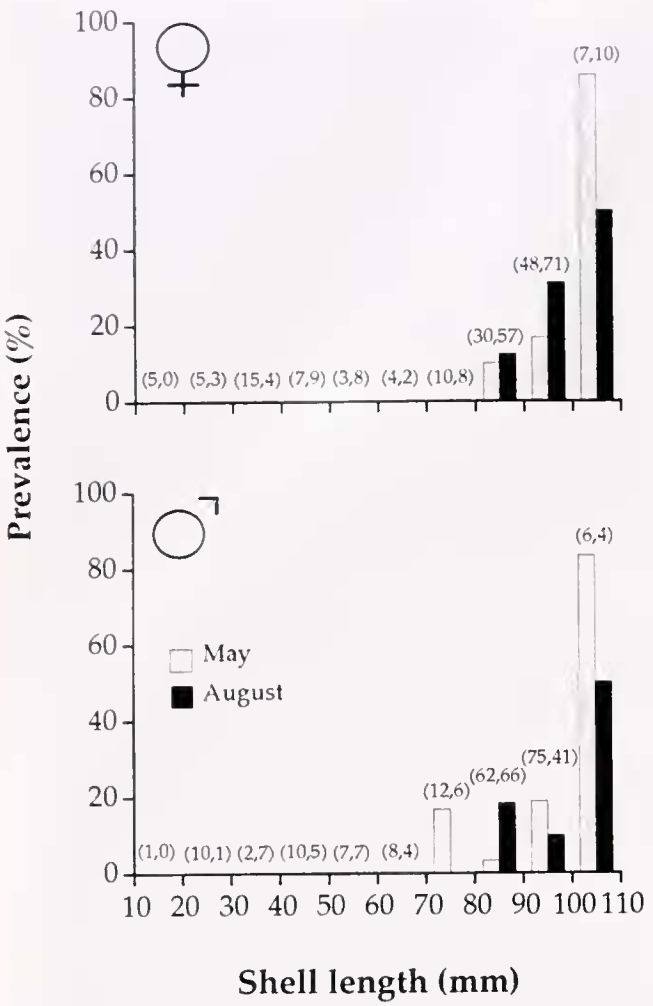

Figure 4. Relation of prevalence (%) of the trematode *Neophasis* sp. in female and male whelks, *Buccinum undatum*, to whelk size for individuals collected in May and August 1994. Numbers in parentheses indicate sample size in May and August, respectively.

these did not contain *Neophasis* sp. or other parasites. The other two were too decomposed to permit adequate examination.

Other parasites

Another trematode, which appeared to also be of the genus *Neophasis*, was observed in the digestive gland of some whelks, but did not affect the appearance of this organ. It probably had little effect on these whelks because the intensity of infection was low, a mean of 1.2 immature trematodes per whelk and a maximum of 3. It was larger (mean body length = 2.36 mm, SE = 0.22) than the cercariae and rediae of the above *Neophasis* species, anterior eyes and a pharynx were visible, and no specimens were observed with a tail. Due to the poor condition of these trematodes, we could not determine if they contained cercariae or if gonads were present. This parasite was found in 5.4% of whelks in May (1 immature female, 1 immature male, 4 adult females, 11 adult males) and 7.9% of whelks in August (9 immature females, 6 immature males, 3 adult females, 5 adult males).

We noted the presence of yellow bodies, 1–2 cm in diameter, in the digestive gland in some whelks (2 females and 3 males in May, 3 females and 1 male in August, and 1 female and 1 male in January 1996). The digestive glands were preserved in 10% formalin. Examination of 5-μm thick sections of digestive glands containing these bodies (stained with hematoxylin-eosin) revealed another trematode within the empty tubules of the digestive gland. It appeared to have the cercarial characteristics of the genus *Renicola*: oral and ventral suckers, a short undivided tail, no stylet or eyes, and the pharynx small or absent. This parasite was previously reported by Koie (1969) for *Buccinum undatum* in Danish waters.

One adult digenetic trematode observed in the stomach of about 12% of the whelks was identified as *Steringophorus furciger*, a parasite previously reported from the stomach of whelks in the Mingan Islands by Hamel (1989) and from the stomach of American plaice in the Gulf of St. Lawrence by Scott (1975) and Scott and Scott (1988).

Discussion

Identification of parasites in the gonad and digestive gland

The adult stage is required for specific identification of *Neophasis*; because we did not succeed in infecting American plaice (*Hippoglossoides platessoides*) with larval

Table 1

Difference between best adjusted models (significant at 5%) relating impact of sex (S) and sampling month (M) to prevalence (P) and proportion of digestive gland occupied (O) by Neophasis *sp.*

Model	df	Log-likelihood ratio LLR	Probability value
Prevalence			
(a) lnE = P + S + M + SM + PM + PS	1	0.15	0.70
difference between (a) and (b)	1	0.18	0.67
(b) lnE = P + S + M + SM + PS	2	0.33	0.85
difference between (b) and (c)	1	1.76	0.18
(c) lnE = P + S + M + SM + PM	2	2.09	0.35
Digestive gland			
(a) lnE = O + S + M + OS + OM + SM	2	2.79	0.25
(b) lnE = O + S + M + OM + SM	4	5.33	0.26
difference between (a) and (b)	2	2.54	0.28

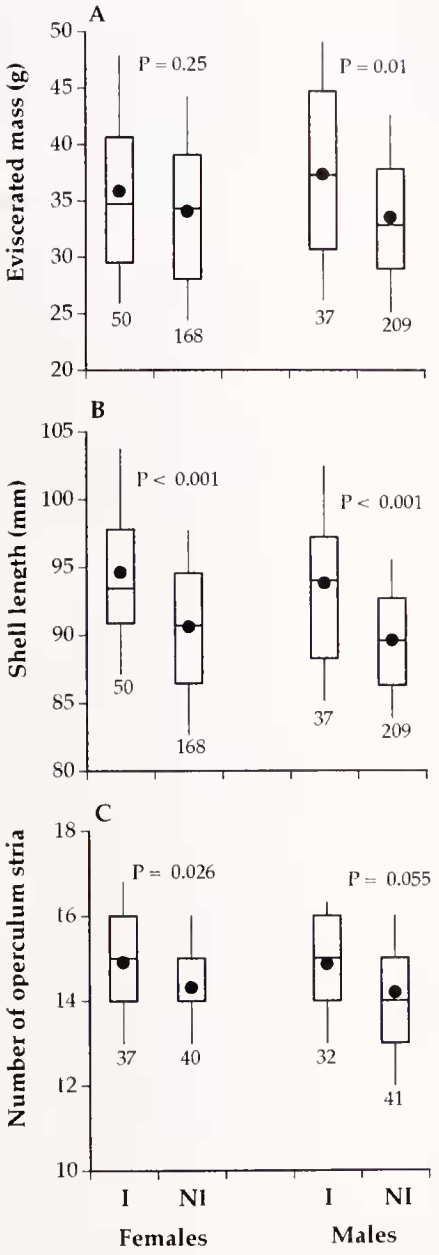

Figure 5. Eviscerated mass (A), shell length (B), and number of operculum striae (C) of female and male whelks, *Buccinum undatum*, infected (I) and noninfected (NI) by *Neophasis* sp., in May and August 1994. The Mann-Whitney *U* test was used to compare the eviscerated mass and shell length of infected and noninfected whelks. Numbers above box plots are probabilities, and numbers below are sample sizes. The top, middle, and lower horizontal lines show the 75th, 50th, and 25th percentiles, respectively. The black circle indicates the mean, and the vertical lines extend from the 10th to the 90th percentiles.

Neophasis sp. from *Buccinum undatum*, we could not determine the species. It is possible that larvae were not infective or that plaice were an unsuitable host. Four species of *Neophasis* Stafford, 1904 [Family: Acanthocolpidae] are described from the North Atlantic: (1) *Neophasis anarrhichae* (Nicoll, 1909) Bray, 1987; (2) *N. burti* Bray and Gibson, 1991; (3) *N. oculatus* (Levinsen, 1881) Miller, 1941; and (4) *N. pusilla* Stafford, 1904 (see Bray and Gibson, 1991, and Gibson, 1996). Bray and Gibson (1991) indicate that *N. burti* may be synonymous with *N. oculatus*, and *N. pusilla* synonymous with *N. anarrhichae*. The species found in whelks in the Mingan Islands may be *N. anarrhichae* since this is the only species thus far described from *B. undatum* (Lebour, 1908, 1911; Køie, 1969; Bray and Gibson, 1991). However, we saw only tailed cercariae, albeit the tails easily detached within redia. Lebour (1910) observed cercariae with and without tails within the same redia (and the tails were easily detached). Køie (1973) rarely found tailed cercaria and considered tailless cercaria as metacercaria that do not encyst but are infective to the final host, as described by Lebour (1910). Possibly, the retention of the tail in cercaria is a function of geographic differences; for example, perhaps in cold Canadian waters the tail is retained longer. *B. undatum* is the only intermediate host, and the final hosts are wolffish of the family Anarhichadidae (*Anarhichas denticulatus*, *A. lupus*, and *A. minor*), which become infected by ingesting parasitized whelks. An abundance of broken whelk shells is usually found at the entrance of dens of *A. lupus* in the Mingan Islands, which suggests that whelks are a major prey (pers. obs.). The final hosts of other species of *Neophasis* are fishes of the families Cottidae, Cyclopteridae, Zoarcidae, and Gadidae (Bray and

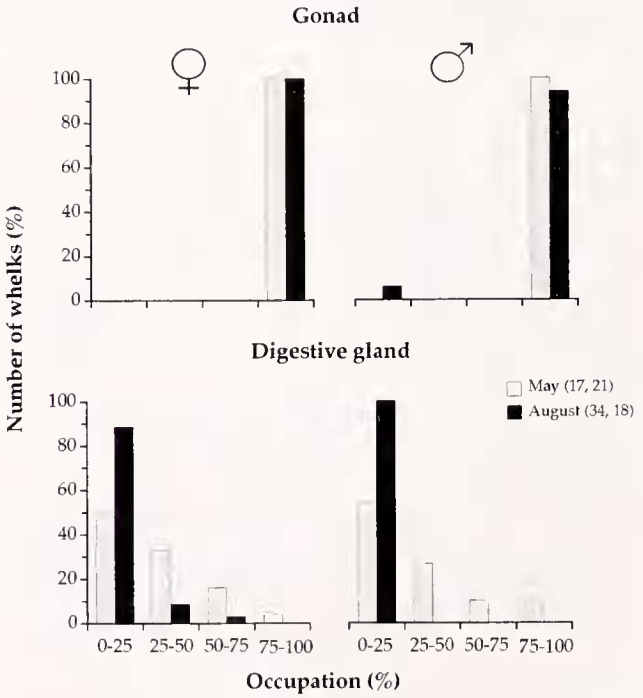

Figure 6. Proportion of the gonad and digestive gland occupied by the trematode *Neophasis* sp. in female and male whelks, *Buccinum undatum*, collected in May and August 1994. Numbers in parentheses indicate the sample size of infected females and males, respectively.

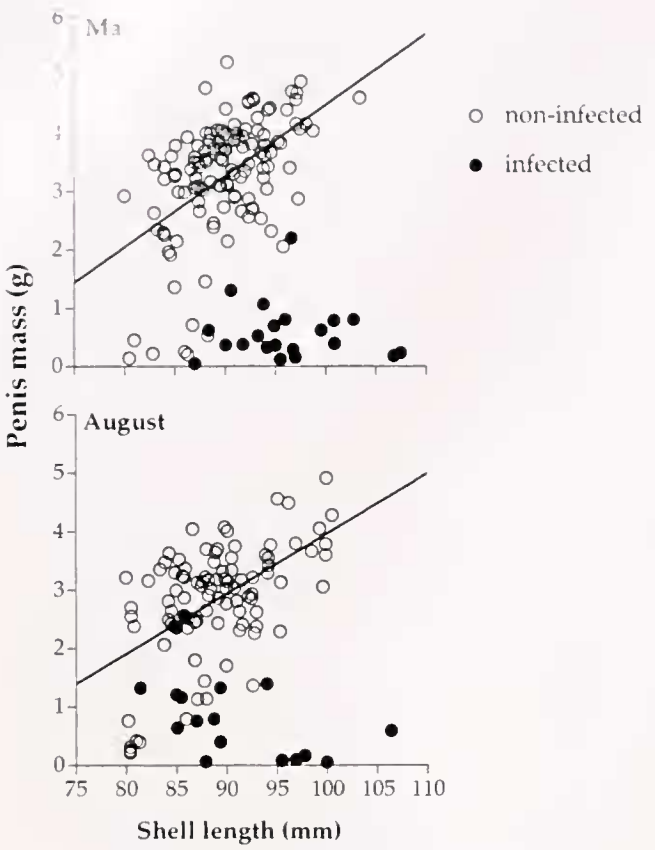

Figure 7. Relation of penis mass to shell length for whelks, *Buccinum undatum*, infected (dark circles) and noninfected (open circles) by the trematode *Neophasis* sp. in samples collected in May and August 1994

Gibson, 1991), and all of the above-mentioned families of fishes are present in the Mingan Islands (Thomas and Himmelman, 1988). Whereas members of the genus *Neophasis* have been reported from American plaice from the North Atlantic (Bray and Gibson, 1991), none have been reported in American plaice or other fishes from the Gulf of St. Lawrence (Scott, 1975). However, *Neophasis* sp. is reported from cod from the southern Gulf of St. Lawrence, although infections were probably accidental (Appy and Burt, 1982). According to Køie (1973), pleuronectiforme fish may acquire *N. anarrhichae*, but the parasites do not mature and infections are lost within a few days.

The persistence of larval *Neophasis* sp. in whelks collected in October 1994 and maintained in the laboratory for 12 to 15 months suggests that the parasite persists in the whelk for long periods. Similarly, Køie (1969) sampled whelks for 12 consecutive months and concluded that the parasite persists in all seasons. Although we did not observe tailless cercariae (metacercariae) during our study, this infective stage may be present in whelks during late winter or early spring.

Prevalence of Neophasis *sp.*

Two hypotheses may explain the increased prevalence of larval *Neophasis* sp. with increasing size for sexually mature whelks (Figs. 4, 5). First, larger whelks may be more frequently infected because they have been exposed to parasites for a longer time. Second, castrating trematodes eliminate energetic demands for reproduction and thereby may increase the growth rate of somatic tissues, a phenomena known as gigantism (*e.g.*, Rothschild, 1936, 1941; McClelland and Bourns, 1969; Mouritsen and Jensen, 1994; Gorbushin, 1997). That the number of opercular striae was greater on infected whelks than on noninfected ones (Fig. 5) suggests that the infected whelks were older, which is consistent with the first hypothesis. If this is true, the hypothesis of gigantism is not necessary to explain the positive relation between size and infection rate. Nevertheless, a comparison of growth rates of infected and noninfected whelks of similar size is needed to provide a more direct test of the gigantism hypothesis.

Gigantism has been reported primarily in short-lived gastropods (Sousa, 1983). Long-lived species, such as *B. undatum*, may devote more energy to tissue repair and may thereby be less likely to display gigantism when parasitized. In whelks in the Mingan Islands, the energy required to repair damage may be high because the redial stages of *Neophasis* digest extracorporally and later absorb host materials through the mouth or tegument (Køie, 1971). Thus, rediae may require more energy from their host than sporocysts that absorb nutrients through the body wall without damaging host tissues (Sousa, 1983; Vernberg and Vernberg, 1974). The effect of parasitic castration on the growth rate of infected individuals may further depend on host population density and parasite species. For instance, Gorbushin (1997) found that the growth rate of *Hydrobia ventrosa* tends to be stunted by the parasitic trematode *Bunocotyle progenetica* when host density is high, but is significantly increased when host density is low. In contrast, under field conditions, trematode species from the families Nocotylidae and Bunocotylidae have no effect on the growth rate of *Hydrobia ulvae* and *H. ventrosa* (Gorbushin, 1997).

We observed a higher prevalence of *Neophasis* sp. in female whelks than in males in May and August 1994 (Fig. 4). Hughes and Answer (1982) found a similar difference between female and male *Littorina littorea* infected by trematodes. Our understanding of prevalence patterns is restricted by the limited knowledge of how *Neophasis* miracidiae infect whelks and of the resistance of whelks to infections. Possible explanations are that females (1) are more exposed to the parasite because their activities differ from those of males (*e.g.*, egg laying; feeding rates possibly vary because of greater reproductive investment, Martel *et al.*, 1986), (2) are less resistant to infections, or (3) retain

infections for a longer period. A greater prevalence of *Neophasis* sp. in females than in males was further observed in the sample collected in October 1994, which was maintained in the laboratory.

Effects of Neophasis *sp. on the whelk*

In the Mingan Islands, *Neophasis* sp. is strongly associated with gonadal tissues of sexually mature whelks. In this respect, it is similar to the trematodes infecting the gastropod *Littorina littorea* (Hughes and Answer, 1982). In contrast, in Denmark, *Neophasis anarrhichae* infects the digestive gland of immature whelks as well as the gonad and digestive gland of mature individuals (Køie, 1969). Studies are needed to elucidate why *Neophasis* sp. is absent in the digestive gland of immature whelks in the Mingan Islands.

In both sampling periods, the gonads of infected whelks were almost completely occupied by the parasite (Fig. 6). This strongly suggests rapid proliferation of the parasite once inside the host. In contrast, the digestive gland was much less infected, and percentage occupation decreased markedly from May to August in both sexes (Fig. 6). The decrease could be due to either tissue repair or mortality of infected whelks. Køie (1971) observed high mortalities of whelks infected with *N. anarrhichae*, suggesting that the animals eventually die from infection. This is also suggested by the massive tissue damage caused by *Neophasis* and because scars, which would indicate healing, have not been observed (Køie, 1971, this study). That we observed no mortality of infected whelks kept in the laboratory for 15 months might have been because food was abundant and predators absent. A number of studies demonstrate a negative effect of trematode parasites on gastropods when environmental conditions are unfavorable (Vernberg and Vernberg, 1963, 1967; Sousa and Gleason, 1989), and some castrating trematodes are known to cause death of their hosts (Stunkard, 1964; Lauckner, 1986). Mortality could be due directly to the parasite or indirectly to predation. Potential predators of adult whelks in the Mingan Islands are numerous and include the asteroids *Leptasterias polaris* and *Asterias vulgaris* (see Dutil, 1988); the common eider, *Somateria mollissima* (see Guillemette *et al.*, 1992); and the wolffish, *Anarhichas lupus*.

Both our study and that of Køie (1969) show that an atrophy of the penis is associated with the presence of castrating trematodes in *Buccinum undatum* (Fig. 7). This probably results from the destruction of the gonad, which produces sexual hormones (Caullery, 1950). The high degree of destruction of the reproductive organs by *Neophasis* sp. makes these organs virtually nonfunctional. Neither our study nor that of Køie (1969) provided evidence that the parasite could cause a change of sex.

Other parasites

The genus *Renicola* was identified in the digestive gland of a small proportion of whelks in our study and in that of Køie (1969). The sporocysts (with cercariae) of the genus *Renicola* infect the digestive gland and gonads of gastropods, causing castration and, in massive infections, death (Stunkard, 1964). Gastropods are the first intermediate host, and cercariae leave through the gills to encyst in the gill tissue of bivalves.

Steringophorus furciger is a trematode parasite usually found in the stomach of flatfish (Scott, 1975; Bray and Gibson, 1980; Scott and Scott, 1988). It feeds on the host's food, and the intensity of the infection can exceed 100 parasites per host individual (Polyanski, 1955). Køie (1969) considered its presence in the stomach of whelks accidental and related to the similar use of food resources by whelks and flatfish. It likely has little effect on whelks from the Mingan Islands because of its low intensity (1–4 parasites per host).

Of the four trematodes infecting *Buccinum undatum* in the Mingan Islands, *Neophasis* sp. clearly has the greatest effect on its host. Although the prevalence of *Steringophorus furciger* was similar to that of *Neophasis* sp., it caused little or no tissue damage and did not invade the gonad. Even though *Renicola* sp. clearly damaged the digestive gland of whelks, its effect on the population is probably negligible owing to its low prevalence. In contrast, *Neophasis* sp. likely markedly affects whelk populations in the Mingan Islands, given that it castrates large numbers of mature individuals.

In undisturbed populations, the relationship between host and castrating parasites normally attains an equilibrium over time, as in prey/predator interactions (Curio, 1988). Additional pressures on host populations, such as those likely to be caused by a fishery, potentially destabilize such relationships. Destabilization is a strong possibility for the whelk/*Neophasis* interaction because both the commercial whelk fishery and *Neophasis* infections reduce the numbers of reproducing whelks.

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